

A NEW SPECIES OF ZAMIA (ZAMIACEAE) FROM THE MAYA MOUNTAINS OF BELIZE

Michael Calonje

Montgomery Botanical Center
11901 Old Cutler Road
Miami, Florida 33156, U.S.A
michaelc@montgomerybotanical.org

Jan Meerman

Green Hills Butterfly Ranch
and Botanical Collections
Cayo District, BELIZE

Patrick Griffith and Geoffrey Hoes

Montgomery Botanical Center
11901 Old Cutler Road
Miami, Florida 33156, U.S.A

ABSTRACT

Zamia decumbens (Zamiaceae), a new species from the Maya Mountains of Belize, is described and illustrated. It has affinity with *Zamia tuerckheimii*, *Zamia bussellii/onan-reyesii*, and *Z. monticola*, to which it is compared.

RESUMEN

Se describe ilustra **Zamia decumbens** (Zamiaceae), una especie nueva de las montañas Maya de Belize. Muestra afinidades con *Zamia tuerckheimii*, *Zamia bussellii/onan-reyesii*, y *Z. monticola*, con las que se compara.

INTRODUCTION

In December of 1997, while conducting research on wild nutmeg trees, John Janovec and Amanda Neill were led to the bottom of a large sinkhole in the Maya Mountains of Belize by naturalist guide Valentino Tzub to look at an interesting group of plants he called “corn palms.” At the bottom of the sinkhole, they found an old Mayan kiln and many pottery shards, and a dense population of *Zamia* (Janovec & Neill 2003). The plants did not match the description of any *Zamia* known from Belize at the time, but shortly after their return, Dr. Dennis Stevenson of the New York Botanical Garden informed them that the holotype of *Zamia prasina* Bull, a species described in 1881 (Bull 1881), had recently been re-discovered at the Kew herbarium. Janovec and Neill (2003) wrote that they connected these specimens to the sinkhole plants, and the name *Zamia prasina* has since been applied to this plant in the horticultural trade and several publications (see Balick 2000; Whitelock 2002).

In August, 2008, Montgomery Botanical Center (MBC) sponsored an expedition to Belize to shed some light on this poorly-known species and other Belizean Zamiaceae. During the course of the expedition, it became clear that the leaflets of these sinkhole-dwelling plants, which were chartaceous, gradually acuminate, with a distinctly raised longitudinal fold, and margins that are entire or with a few minute teeth at the apex, were very different from the leaflets of the *Z. prasina* holotype, which were coriaceous, abruptly acuminate, strongly serrulate and lacking a longitudinal crease. We determined that *Z. prasina* was in fact a prior valid name for *Z. polymorpha* D.W. Stev., A. Moretti & Vázq. Torres (see Calonje et al., pages 43 – 49, this volume), and that the cycads found in the sinkhole belonged to an undescribed species.

During the cycad research expedition, the authors studied four separate populations of this species in Belize, gathering enough data to formally describe it.

SPECIES DESCRIPTION

Zamia decumbens Calonje, Meerman, M.P. Griff. & Hoes, sp. nov. (**Figs. 1–3**). TYPE: BELIZE. TOLEDO DISTRICT: bottom of sinkhole, 350–400 m, 2 Sep 2008, M. Calonje, J. Meerman & P. Griffith BZ08-201 (HOLOTYPE: BRH; ISOTYPES: FTG, MO, NY, XAL).

Species *Z. tuerckheimii* Donn.Sm. affinis sed caule decumbente et pedunculo pollinis longissimo.

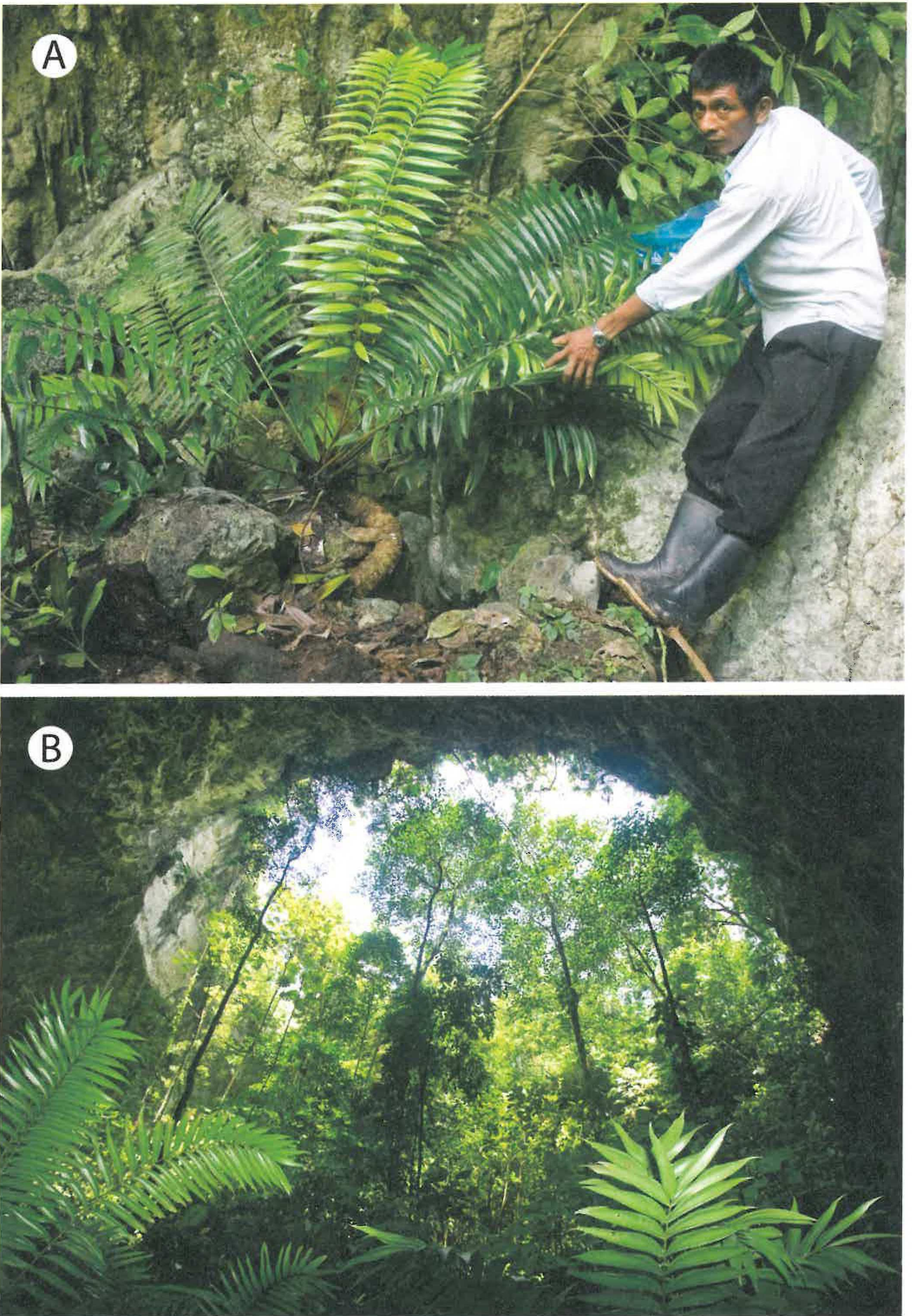


FIG. 1. Habit and habitat of *Z. decumbens*. A. Adult female plant with naturalist guide Valentino Tzub. B. View from sinkhole bottom at type locality of *Z. decumbens*.

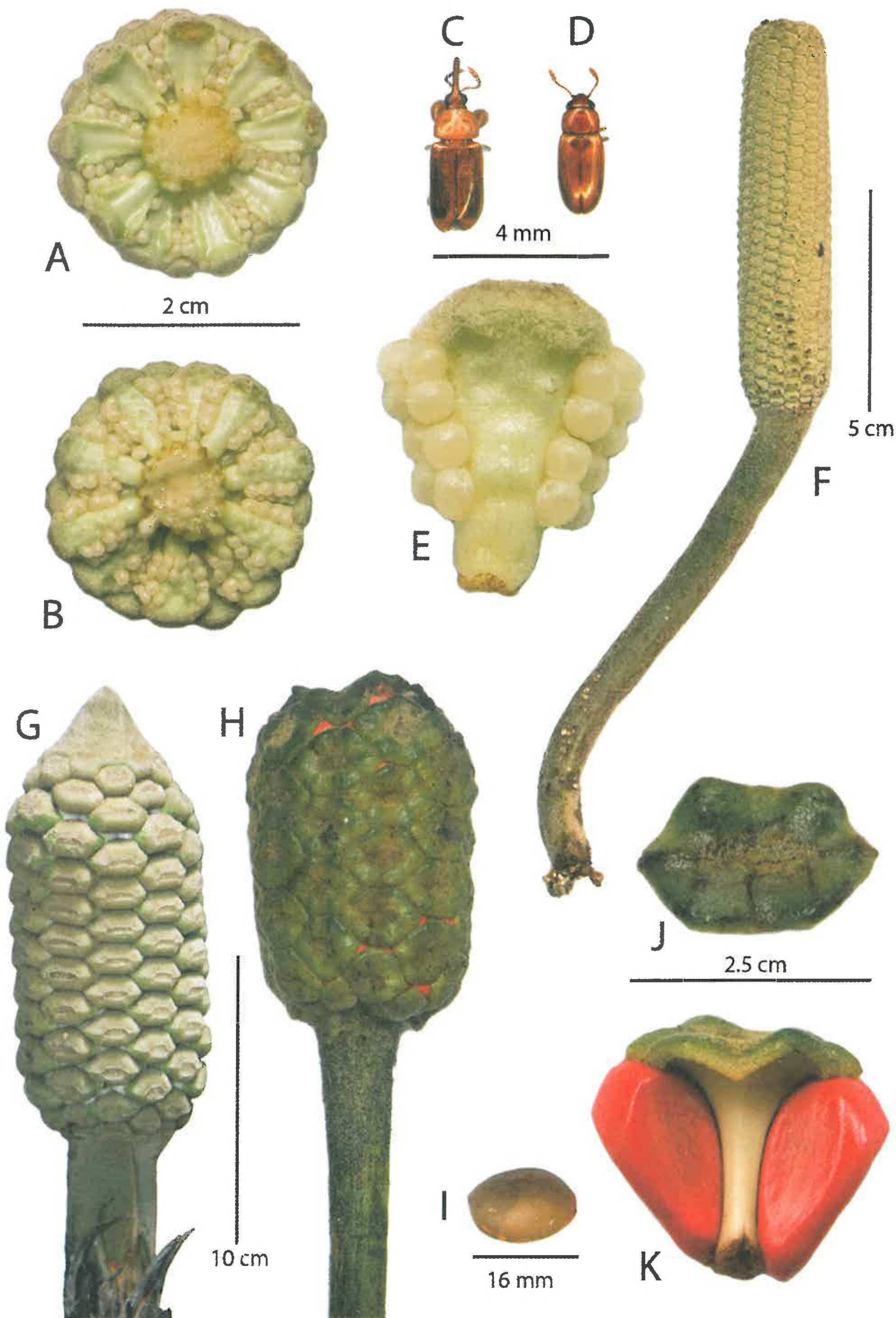


FIG. 2. Reproductive features of *Z. decumbens*. All photographs derived from type locality population. A. Cross section of microsporangiate strobilus, adaxial side. B. Cross section of microsporangiate strobilus, abaxial side. C. *Rhopalotria* sp., putative pollinator of *Z. decumbens*. D. *Pharaxonotha* sp., putative pollinator of *Z. decumbens*. E. Microsporophyll, abaxial side. F. Microsporangiate strobilus. G. Megasporangiate strobilus at pollen receptivity stage. H. Mature megasporangiate strobilus. I. Seed with sarcotesta removed. J. Megasporophyll face. K. Megasporophyll with mature seed, abaxial side.

Stems globose to cylindrical, to 80 cm long and 6.7–11 cm wide, decumbent and occasionally branching on older plants, in habitat often rotting at base and rooting adventitiously from along the horizontal stems. Vegetative cataphylls tan-tomentose, chartaceous, stipulate, shallowly triangular to triangular with short, brown apex; strobilar cataphylls tan-tomentose, chartaceous, narrowly triangular with elongated light-tan lanceolate apex. Leaves on adult plants 5–17 per crown, erect or arching, 90–175 cm long, light green when emerging, turning dark green when mature. Petiole 30–55 cm long with abruptly swollen base 2.2–3.2 cm wide, moderately to heavily armed with prickles up to 5.3 mm long. Rachis 60–120 cm long, unarmed or sparsely armed in the proximal third. Leaflets to 28 pairs per leaf, 2.8–4.1 cm wide, 17.5–29 cm long, spaced 2–5.5 cm apart from each other with the point of attachment to the rachis 4.5–6 mm wide, chartaceous, lanceolate with gradually tapering apex and distinct longitudinal furrow, straight or slightly falcate, margins entire or with a few teeth restricted to apex. Eophylls typically with a single pair of ovate leaflets. Microsporangiate strobilus conical-cylindrical, emerging erect with peduncles progressively leaning outward horizontally, at pollen release 10–16.5 cm long, 2.1–2.5 cm diam., occurring individually or in groups of 2–6 or more, cream to brown; peduncle 12–23 cm long, 0.9–1 cm diam., green with brown pubescence. Microsporophylls arranged in 16–18 columns, 26–36 rows; obtrullate, distal face hexagonal to oblong-hexagonal, 3.0–3.5 mm wide, 4.0–4.5 mm tall; microsporangia spheroidal, 1–1.2 mm diam., present on abaxial surface, absent on adaxial surface, 12–18 per microsporophyll arranged in two separate groups along margins. Megasporangiate strobilus cylindrical, solitary, erect at maturity, 12–20 cm long, 5.7–6.4 cm diam., emerging cream-colored tomentose and maturing to glabrous light or dark green with patches of tan tomentum remaining on inner facet and margins of megasporophylls; peduncle 7–13 cm long, 1.5–2 cm wide, green to brown tomentose. Megasporophylls arranged in 8–12 columns, 4–16 rows; distal face hexagonal to oblong-hexagonal, 2.25–2.9 cm wide, 1.6–1.8 cm tall, 2.5–4 mm thick, with a depressed terminal facet 9.5–12 mm wide, 3.5–4.55 tall. Seeds with sarcotesta ovoid to ovoid-pyramidal, red at maturity, 1.7–2.0 cm long, 1.1–1.45 cm wide; sclerotesta ovoid to ovate, 1.45–1.65 cm long, 1.05–1.43 cm wide.

Other vouchers examined: **BELIZE. Cayo District:** 170–200 m, 19 Aug 2008, M. Calonje, J. Meerman, M.A. Perez-Farrera, B. Arevalo BZ08-040 (FTG), BZ08-041 (FTG), BZ08-053 (BRH). **Toledo District:** 100–200 m, 9, 11, 12 Mar 1987, Davidse & Brant 32232 (MO); bottom of sinkhole, 700 m, 3 Oct 1999, Janovec & Neill 1185, 1186 (FTG). bottom of sinkhole, 300–320 m, 1 Sep 2008, M. Calonje & P. Griffith BZ08-180 (FTG), BZ08-189 (FTG), BZ08-194 (FTG); bottom of sinkhole, Toledo District, 700 m, 2 Sep 2008, M. Calonje, P. Griffith, J. Meerman, & V. Tzub BZ08-222 (FTG), BZ08-224 (FTG), BZ08-225 (FTG), BZ08-227 (FTG), BZ08-231 (BRH), BZ08-232 (FTG); 350–400 m, 2 Sep 2008, M. Calonje, J. Meerman & P. Griffith BZ08-180 (FTG), BZ08-189 (FTG), BZ08-194 (FTG), BZ08-202 (FTG).

Etymology.—The specific epithet refers to the decumbent habit of the stems.

Distribution and habitat.—Known from several locations in the Maya Mountains of Belize in Toledo, Cayo, and Stann Creek districts at elevations of 150–700 m. Currently considered a Belizean endemic, but some populations occur near the border with Guatemala, and since the Maya Mountains extend into South-eastern Petén Province, it is likely to occur here as well. These locations were within Tropical Evergreen Broadleaf Lowland Forest variants as defined by Meerman and Sabido (2001) and over a number of geological formations, most notably late Cretaceous limestones, but also older Triassic metamorphic bedrock to a lesser extent (Cornec 2003).

The authors have observed seven different occurrences of this species found throughout the Maya Mountains of Belize, encompassing an area of approximately 2600 km². However, each of these populations was extremely small and restricted to rocky mountaintops and ridges or on the bottom of sinkholes. The largest populations found have been inside two steep-walled sinkholes in Toledo district, each approximately 50–80 m wide and 30–60 m in depth, with approximately 150 large plants of reproductive age. The mountaintop and ridge populations observed to date have been much smaller, with a maximum of 20 plants observed, all much smaller in size than those observed in the sinkholes. The factor limiting the distribution of this species appears to be reduced soil moisture. In the sinkholes, the plants are found growing near the sinkhole walls within the sinkhole overhang drip line, where there is less light and they are protected from direct rainfall. Few other plant species are present in these areas, in low densities, with large areas of unoccupied soil (Table 1). The mountaintop populations may benefit from the quick-draining substrate provided by

TABLE 1. Associated vegetation observed within dry area of sinkhole in the type locality for *Zamia decumbens*.

Taxon	Family
<i>Justicia</i> sp.	Acanthaceae
<i>Louleridium donnell-smithii</i>	Acanthaceae
<i>Adiantum macrophyllum</i>	Adiantaceae
<i>Syngonium podophyllum</i>	Araceae
<i>Chamaedorea geonomiformis</i>	Arecaceae
<i>Aristolochia veracruzana</i>	Aristolochiaceae
<i>Forchhammeria trifoliata</i> var. <i>trifoliata</i>	Capparidaceae
<i>Tradescantia spathacea</i>	Commelinaceae
<i>Dracaena americana</i>	Dracaenaceae
<i>Acalypha macrostachya</i>	Euphorbiaceae
<i>Episcia punctata</i>	Gesneriaceae
<i>Calatola laevigata</i>	Icacinaceae
<i>Dorstenia lindeniana</i>	Moraceae
<i>Ficus</i> sp.	Moraceae
<i>Passiflora lancetillensis</i>	Passifloraceae
<i>Peperomia</i> sp.	Piperaceae
<i>Piper</i> spp.	Piperaceae
<i>Deherainia smaragdina</i> var. <i>smaragdina</i>	Theophrastaceae
<i>Myriocarpa heterostachya</i>	Urticaceae
<i>Myriocarpa longipes</i>	Urticaceae
<i>Urera baccifera</i>	Urticaceae

the rocky environment. In Toledo district, other lithophytic species such as *Chamaedorea adscendens* and *Chamaedorea schippii* were also observed growing in the same environment.

Climate—The average annual precipitation within this species' range is estimated at 1800–2800 mm, with a distinct dry season occurring from February through May. The wettest month is July, with an average monthly range of 205–580 mm; the driest month is April, with a range of 50–70 mm. The temperature ranges from 16–31°C, with an annual mean temperature of 22–25°C. The coldest month is January and the warmest month is May (data derived from GIS analysis using Worldclim 1.4 climate layers as described by Hijmans et al. (2005)).

Reproductive phenology.—The reproductive phenology of this little-studied species is not well known and no distinct periodicity is evident based on the authors' visits in September of 2008, as well as the examination of photographic evidence archived at Montgomery Botanical Center from John Janovec and Amanda Neill's visits to the sinkhole populations in August of 1999, and June of 2001. Immature, pollen-releasing, and old microsporangiate strobili were observed during all three visits. Receptive megasporangiate strobili were observed in August and September, and near-mature strobili were observed in June and September.

Ecology.—Several microsporangiate strobili at pollen-release stage observed at both sinkhole localities harbored numerous snout weevils of an unknown *Rhopalotria* species, as well as clavicorn beetles of an unknown *Pharaxonotha* species (Fig. 2c, d). Both genera are believed to be pollinators of *Zamia* and have previously been found in microsporangiate strobili of *Zamia furfuracea* L.f. (Vovides 1991) and *Z. pumila* L. (Tang 1987), as well as entering and exiting both microsporangiate and megasporangiate strobili in many natural *Zamia* populations in Panama (Alberto Taylor, pers. comm.). A preliminary examination of the *Rhopalotria* insects suggests that they are either conspecific or close relatives to *Rhopalotria mollis*, one of the known pollinators of *Zamia furfuracea* L.f. (William Tang, pers. comm.).

Ceratozamia robusta Miq. occurs throughout the range of *Z. decumbens* and both species were observed growing sympatrically at one location in Northern Cayo district. *Zamia decumbens* was also observed growing together with *Zamia variegata* Warsz. at one location in southern Toledo district, with no evidence of hybridization. These two species are unlikely to overlap much geographically, as most observed populations of *Z. decumbens* occur above 300 m, which is the maximum of the altitudinal range of *Z. variegata*.

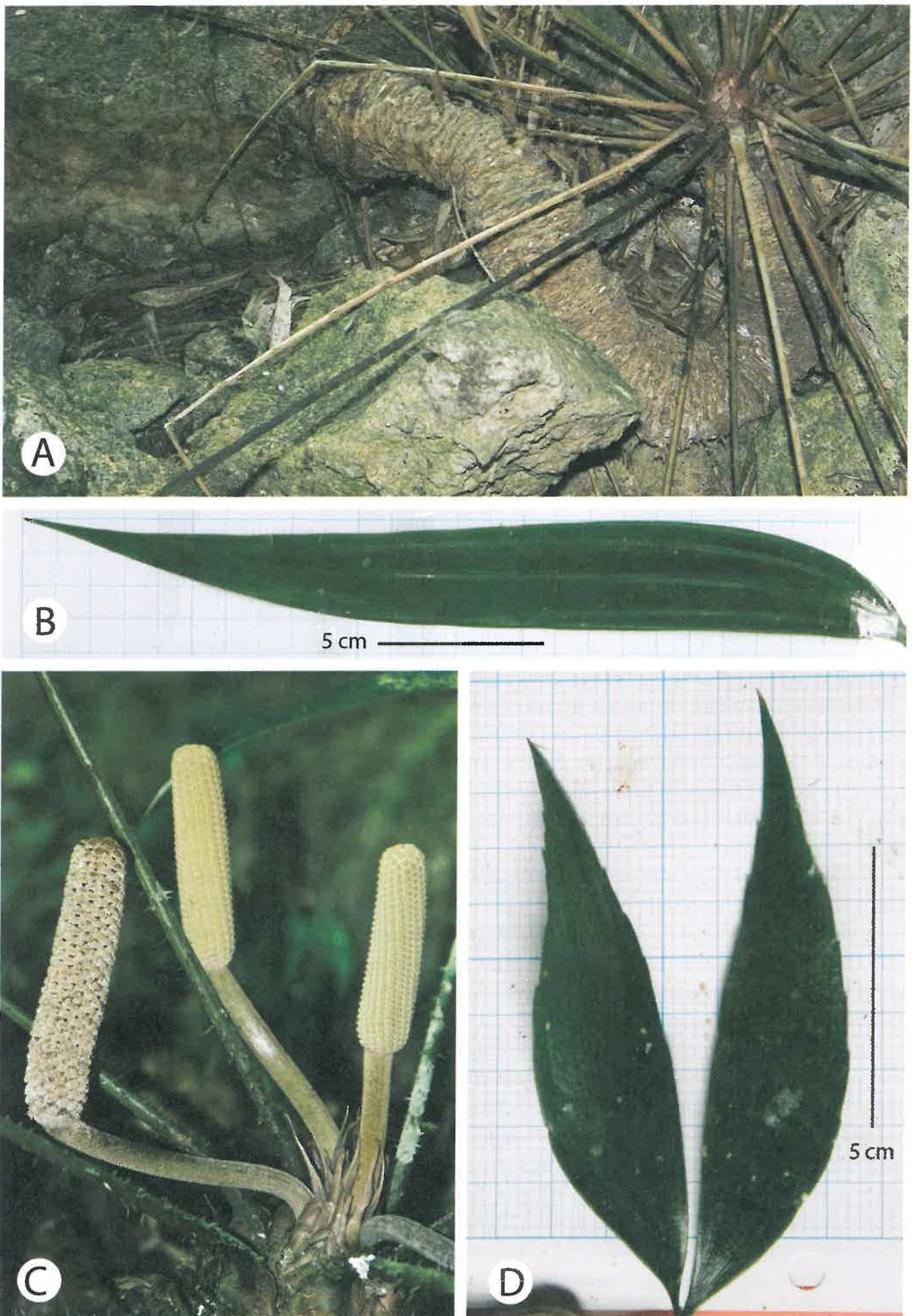


FIG. 3. Diagnostic characters of *Z. decumbens*. All photographs derived from type locality population. A. Decumbent stem with rotted base. Notice decomposition stain on rock behind. B. Typical median leaflet. C. Long-pedunculate leaning microsporangiate strobili. D. Eophylls.

DISCUSSION

Zamia decumbens appears to be most closely related to *Zamia tuerckheimii* Donn.Sm. from Guatemala as well as a new species described from Honduras. The taxonomic priority for this Honduran species, described separately as *Zamia bussellii* Schutzman, R.S. Adams, J.L. Haynes & Whitelock and *Z. onan-reyesii* C. Nelson & Sandoval is currently in dispute and will therefore be treated here as *Z. bussellii/onan-reyesii*.

Zamia decumbens differs from both species in having decumbent stems to 80 cm long that often rot at the base and re-root horizontally. *Zamia tuerckheimii* has erect or leaning stems to 3 m tall, and *Z. bussellii/onan-reyesii* has erect or leaning stems to 2 meters tall. All three species have leaflets with a marked longitudinal crease most prominent near the point of attachment to the rachis, but the leaflets of *Z. bussellii/onan-reyesii* are characteristic enough to distinguish it vegetatively from the two other species (Fig. 4). *Zamia bussellii/onan-reyesii* leaflets are papyraceous and with prominent teeth on the lower margin compared to those of the other two species, which are chartaceous with margins entire or minutely toothed at the apex. Leaflets of *Z. decumbens*, measuring 2.8–4.1 cm in width, are typically narrower than those of *Z. tuerckheimii*, which typically measure 4–9 cm in width. Another useful vegetative distinction between the two species is that *Z. decumbens* has moderately to heavily armed petioles whereas those of *Z. tuerckheimii* are unarmed or sparsely armed.

Mature microsporangiate strobili of *Zamia decumbens* are easily distinguished from those of the two other species as they have long peduncles 11–23 cm in length causing them to lean outward, whereas *Z. tuerckheimii* has erect to slightly leaning strobili with peduncles to 6.5 cm long and *Z. bussellii/onan-reyesii* has erect to slightly leaning strobili with peduncles to 8.5 cm long. *Zamia bussellii/onan-reyesii* has the largest microsporangiate strobili, measuring up to 27.5 cm long and 3.8 cm in diameter, whereas those of *Z. tuerckheimii* measure 14–17 cm in length and 2.5 to 4 cm in diameter, and those of *Z. decumbens* measure 10–16.5 cm. *Zamia bussellii/onan-reyesii* is further differentiated from the other two species because it has more than 40 microsporangia arranged in a single group on the abaxial surface of the microsporophyll whereas *Z. decumbens* has 12–18 microsporangia arranged in two separate groups and *Z. tuerckheimii* has 18–26 microsporangia arranged in two separate groups. The microsporophylls of *Z. tuerckheimii* are elongate triangular, approximately 1.8–2.5 times as long as they are wide, whereas those of *Z. decumbens* and *Z. bussellii/onan-reyesii* are roughly triangular and approximately 1.3 to 1.5 times as long as they are wide.

The megasporangiate strobili of *Z. bussellii/onan-reyesii* are the largest of the group, measuring 22.4–25.2 cm tall and 10–11.2 cm wide with sporophylls faces 4.5–5 cm tall and 4.3–4.6 cm wide, compared to those of *Z. tuerckheimii* which are 16.3–22 cm tall and 8.3–10 cm wide with sporophyll faces 1.8–2.2 cm tall and 2.3–3.8 cm wide, and to those of *Z. decumbens* which are 12–20 cm tall and 5.7–6.4 cm wide with sporophyll faces 1.6–1.8 cm tall and 2.25–2.9 cm wide. See the following dichotomous key and Table 2 for summary of diagnostic characters. The known geographical ranges of the three species do not overlap (Fig. 5).

KEY TO *Z. BUSSELLII/ONAN-REYESII*, *Z. DECUMBENS*, *Z. TUERCKHEIMII*

1. Leaflets papyraceous with prominent teeth on lower margin _____ **Z. bussellii/onan-reyesii**
1. Leaflets chartaceous with entire margins or minutely toothed at the apex.
 2. Stem decumbent, microsporangiate strobili peduncle 11–23 cm long _____ **Z. decumbens**
 2. Stem erect or leaning, microsporangiate strobili peduncle to 6.5 cm long _____ **Z. tuerckheimii**

One other species, *Zamia monticola* Chamb. appears to share some similarities with *Z. decumbens* in leaf length, leaflet shape and size, and microsporangiate strobilus size. It was described by Charles J. Chamberlain based on a single male plant cultivated from seed reportedly collected near Naolinco Crater in the vicinity of Xalapa, Mexico. Chamberlain (1926) contends that the single plant sprouted from a batch of seeds thought to be *Ceratozamia mexicana*. The species has never been found again in the area where it was reportedly collected, and it is thought that it is either extinct, or that Chamberlain's seeds became mixed in his glasshouse and this species was acquired elsewhere (Hill 2004). Material collected in southern Alta Verapaz in Guatemala is currently being identified as this species, but this Guatemalan material is poorly

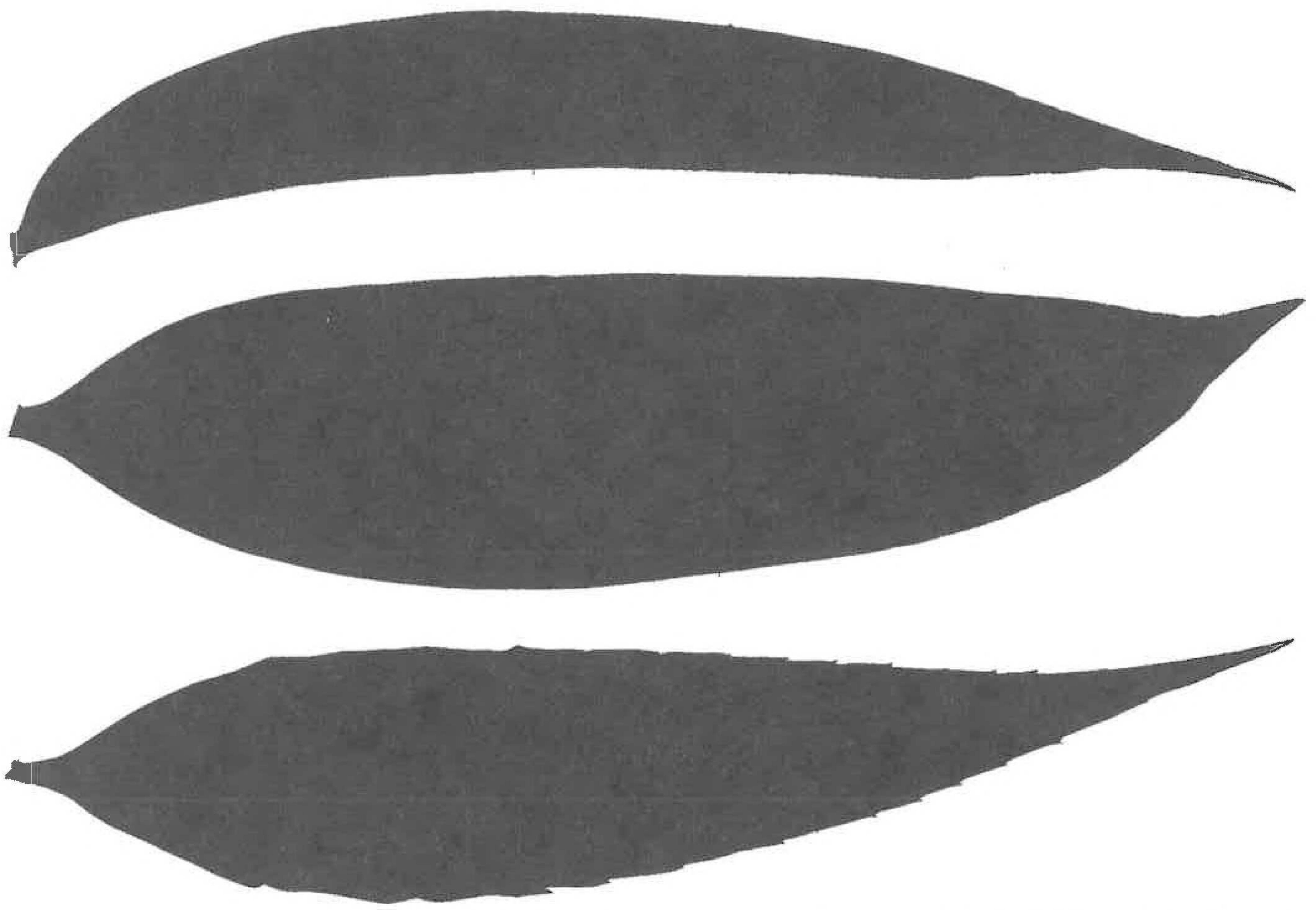


FIG. 4. Leaflet shape comparison. From top to bottom: *Zamia decumbens*, *Zamia tuerckheimii*, *Zamia bussellii/onan-reyesii*.

understood at this time. Considering the fact that the species was described from a single cultivated individual obtained under unusual circumstances, that its present geographic distribution remains unclear, and that its megasporangiate strobili are unknown, a detailed comparison cannot currently be made between this species and *Z. decumbens*. However, based on Chamberlain's description, this species appears to have an erect stem 14 cm in diameter compared to the stems of *Z. decumbens*, which are decumbent and up to 11 cm across. In addition, *Z. monticola* is described as having 20–32 microsporangia per microsporophyll, whereas *Z. decumbens* has 12–18.

Conservation status.—Although we observed seven different populations in the Maya Mountains adding up to an extent of occurrence of 2600 km², the populations were all small, occupying a small area, and limited to the very specialized mountain top and sinkhole habitats. Despite visiting seven populations, only the two sinkhole populations had numerous large plants of reproductive size (about 150 each). The rest of the populations, located on rocky mountaintops, all had less than 15 individual plants of a much smaller size than those observed in the sinkholes. In total, less than 350 plants were observed within a combined area of occupancy of less than a square kilometer. Discussion with local residents throughout the range of *Z. decumbens* confirms that plants of this species have been extracted commercially in the past and seeds continue to be extracted for commercial purposes. During our fieldwork in the sinkholes, we found evidence of past mechanical removal of megasporangiate strobili, and a seemingly low number of seedling and young plants, perhaps suggesting that continued harvesting of seeds may be affecting the health of these populations. Specific locality information has been purposefully withheld from this paper in order to further minimize the risk of illegal harvesting.

Considering how fragmented the distribution of this species is, most likely resulting from its specific habitat requirements, the small number of healthy, reproductively active populations observed, the small combined area of occupancy for this species, and the evidence of past and present commercial exploitation,

TABLE 2. Summary of diagnostic characters for *Z. tuerckheimii*, *Z. bussellii/onan-reyesii*, and *Z. decumbens*.

	<i>Z. tuerckheimii</i>	<i>Z. bussellii/onan-reyesii</i>	<i>Z. decumbens</i>
Microstrobilus length	14–17 cm	27.5 cm	11–16.5 cm
Microstrobilus width	2.5–4 cm	3.8 cm	2.1–2.5 cm
Microstrobilar peduncle length	to 6.5 cm	8.5 cm	11–23 cm
Microsporophyll shape	Elongate triangular	Broadly triangular	Broadly triangular
Microsporangia	18–26 Arranged in two rows	40+ arranged in single row	12–18 arranged in two rows
Megastrobilus length	16.3–22 cm	22.4–25.2 cm	12–20 cm
Megastrobilus width	8.3–10 cm	10–11.2 cm	5.7–6.4 cm
Leaf length	to 2 m	to 1.51 m	to 1.75 m
Leaf number	to 20	to 40	to 17
Petiole armature	Sparse or unarmed	Light to moderate	Moderate to heavy
Leaflet length	19–30 cm	15.5–36 cm	17.5–29 cm
Leaflet number	to 14	to 23	to 28
Leaflet width	4–9 cm	3–4.4 cm	2.8–4.1 cm
Leaflet texture	Chartaceous	Papyraceous	Chartaceous
Leaflet margins	Entire or with a few minute teeth at distal end	Prominent teeth on the lower margin	Entire or with a few minute teeth at distal end
Eophyll leaflet pairs	1	4	1
Stem height	to 3 m	to 2 m	to 80 cm long.
Stem habit	Erect or leaning	Erect or leaning rotting at base and rooting horizontally	Decumbent, often

Zamia bussellii/onan-reyesii measurements derived from Schutzman et al., 2008. *Zamia tuerckheimii* measurements derived from Donnell Smith (1903), Standley & Steyermark (1958), Vannini 2008, and measurements taken by primary author. *Zamia decumbens* measurements taken *in-situ* by authors. All measurements based on mature plants.

we consider this species critically endangered and therefore recommend a Red List Category of CR for this species based on criteria B2ab (i, ii, iii, iv, v) (IUCN 2001). It should be noted that although the criteria have changed somewhat based on new information, we are recommending a continuation of the Red List category currently listed for this species under the misapplied name “*Zamia prasina*.”

ACKNOWLEDGMENTS

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John Janovec and Amanda Neill were the first to scientifically document and collect the sinkhole populations of *Z. decumbens*, providing the inspiration for our return to Belize on a research expedition. Green Hills Butterfly Ranch and Botanical Collections donated significant in-kind support by providing lodging, equipment and work infrastructure in Belize. The Belize Forest Department granted the scientific research and collecting permit (CD/60/3/08(45)) supporting research on Belizean Zamiaceae, as well as herbarium infrastructure for preservation of voucher specimens. Valentino Tzub and Boris Arevalo provided field assistance. Willie Tang offered to identify the possible pollinators of *Z. decumbens* and provided the images of them. Jay Vannini provided information on *Z. tuerckheimii* and comments on the manuscript. Bart Schutzman helped in the Latin diagnosis and provided comments on the manuscript. Anders Lindstromm, Chad Husby, and Alberto Sidney Taylor provided comments on the manuscript. Nancy Korber provided assistance in locating hard-to-find references. Dennis Stevenson provided herbarium specimen images and references.

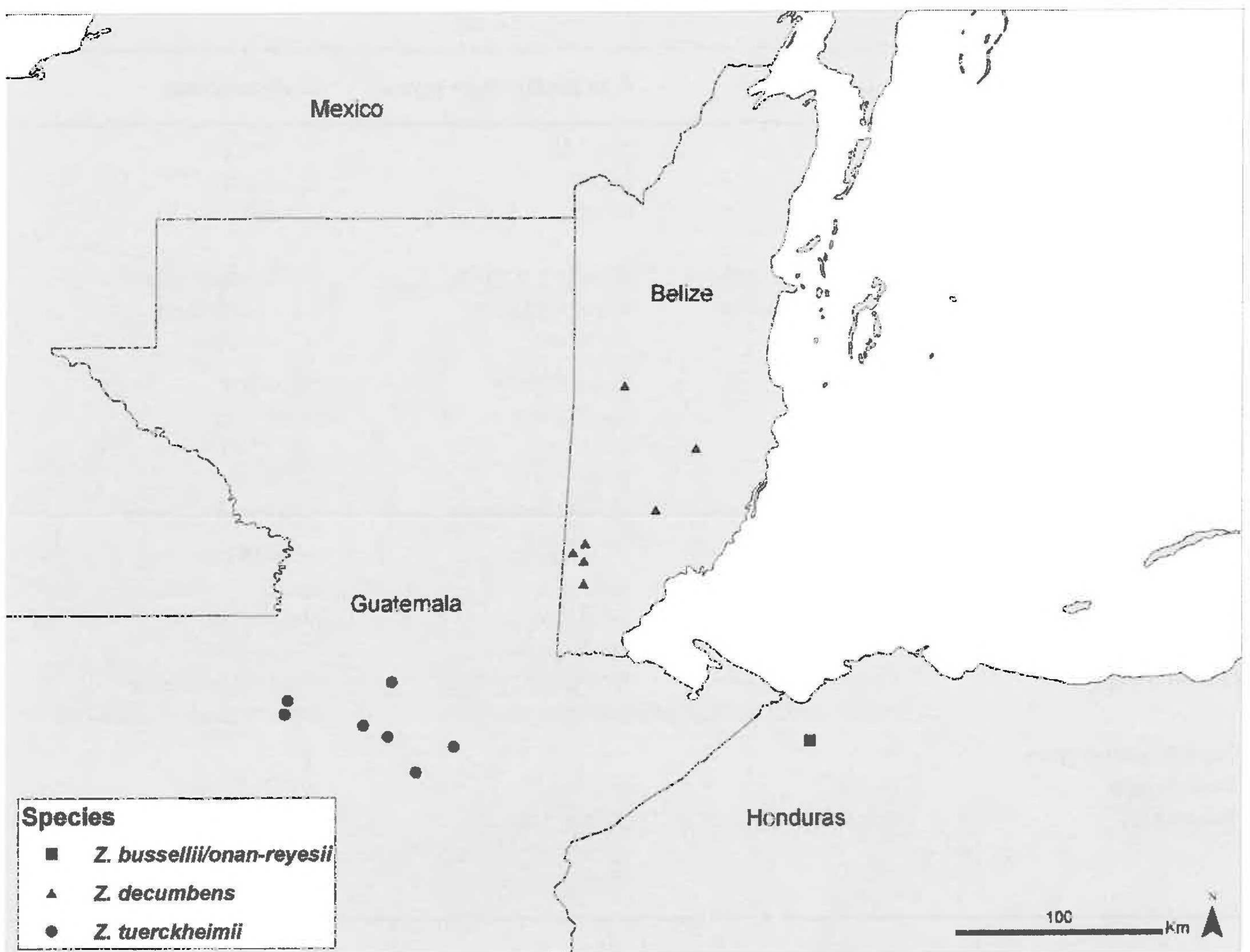


FIG. 5. Geographical distribution of *Z. bussellii/onan-reyesii*, *Z. decumbens*, and *Z. tuerckheimii*.

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